FLEXIBILITY OF FORAGING BEHAVIOR IN HUMMINGBIRDS: THE ROLE OF ENERGY CONSTRAINTS AND COGNITIVE ABILITIES

Paulina L. González-Gómez,[1,2,5] Rodrigo A. Vásquez,[3] and Francisco Bozinovic[4]

[1]*Department of Neurobiology, Physiology, and Behavior, 1 Shields Avenue, University of California, Davis, California 95616, USA;*
[2]*Instituto de Filosofía y Ciencias de la Complejidad (IFICC), Los Alerces 3024, Santiago, Chile;*
[3]*Instituto de Ecología y Biodiversidad (IEB), Departamento de Ciencias Ecológicas, Facultad de Ciencias,*
Universidad de Chile, Casilla 653, Santiago, Chile; and
[4]*Centro de Estudios Avanzados en Ecología and Biodiversidad (CASEB), LINC-Global and Departamento de Ecología,*
Pontificia Universidad Católica de Chile, CP 6513677, Santiago, Chile

Abstract.—We assessed how individual foraging preferences and cognitive performance affect foraging bout interval and the flexibility of foraging behavior in the nectarivorous Green-backed Firecrown (*Sephanoides sephaniodes*). Our field experiment evaluated the ability of these hummingbirds to recall nectar-renewal rates in two groups of artificial flowers with the same nectar concentration in the absence of visual cues. In a second experiment, we assessed their ability to remember differences in nectar quality combined with different nectar-renewal intervals, given artificial flowers with identical visual cues. Our results indicate that Green-backed Firecrowns adjusted their foraging intervals according to nectar-renewal rates and, furthermore, that birds were able to recall nectar concentration as well as nectar-renewal rate. Individual differences in memory performance resulted in differences in energy intake. These results strongly suggest that individual preferences and individual cognitive performance could play a central role in energy intake and, therefore, in the probability of survival. *Received 30 September 2009, accepted 27 October 2010.*

Key words: behavioral ecology, energetics, individual performance, memory, renewal rate.

Flexibilidad de la Conducta Alimenticia en los Picaflores: El Rol de las Restricciones Energéticas y de las Habilidades Cognitivas

Resumen.—Evaluamos cómo las preferencias en el forrajeo y el desempeño cognitivo afectan los intervalos de forrajeo y la flexibilidad en la conducta alimenticia de *Sephanoides sephaniodes*. En nuestro experimento de campo evaluamos la habilidad de *S. sephaniodes* para recordar las tasas de renovación de néctar en dos grupos de flores artificiales con la misma concentración de néctar en ausencia de pistas visuales. En el segundo experimento determinamos la capacidad de los picaflores de recordar diferencias en calidad de néctar asociada con diferentes intervalos de renovación de néctar en flores artificiales con idénticas características visuales. Nuestros resultados indican que *S. sephaniodes* ajusta sus intervalos de forrajeo de acuerdo a las tasas de renovación de néctar y que los individuos son capaces de recordar tanto la concentración como la tasa de renovación del néctar. Las diferencias individuales en la memoria resultaron en diferencias en la energía obtenida. Nuestros resultados sugieren fuertemente que las preferencias individuales y el desempeño cognitivo jugarían un rol clave en la obtención de energía y, por lo tanto, en la probabilidad de supervivencia.

It is generally accepted that physiology modulates foraging behavior by a variety of mechanisms. For example, enzymatic activity and intestinal processing time can limit foraging options and influence the choice of foods to include in the diet and foraging frequency (Diamond et al. 1986, Martínez del Rio and Stevens 1989, Martínez del Río and Karasov 1990). However, the effect of individual foraging preferences on foraging frequencies, the influence of individual cognitive performance on foraging frequencies, and the degree of flexibility of individual foraging behavior have received little attention despite the fact that they are probably closely linked to the survival (i.e., fitness) of individuals.

Hummingbirds that inhabit temperate zones provide an excellent model system to study these issues because of the diverse factors that converge to shape their foraging ecology. For example, they experience physiological and ecological constraints on food harvesting and exceptionally high metabolic demands because of their small body size and low environmental temperatures (Fernández et al. 2002). The maintenance of high and constant

body temperature is expensive for small endothermic organisms (Bicudo 1996); thermoregulatory costs for small birds can account for 40–60% of their total daily energy budget (Lasiewski 1963, Wolf et al. 2000). Moreover, the hovering flight of hummingbirds is the most energetically expensive flight style, and the convective cooling produced by their rapid wing beats may further exacerbate heat loss and energy demands (Chai et al. 1998). In order to meet these high energy demands, hummingbirds must ingest large quantities of high-quality nectar (Lotz et al. 2003). Although energy assimilation in hummingbirds may be limited more by crop emptying time and digestive processes than by food collection (Diamond et al. 1986, Karasov et al. 1986, McWhorter and Martínez del Río 2000), flowers may impose constraints on nectar harvesting (Stephens et al. 2007). For instance, the availability of nectar varies throughout the day, as do nectar-replenishment rates (McDade and Weeks 2004). The flowers that hummingbirds feed on can have nectar concentrations that fluctuate >9 times in concentration and >300 times in quantity over the course of a day (P. L. González-Gómez unpubl. data).

Hummingbirds are able to efficiently exploit nectar sources in part because they can remember the highest sucrose concentrations among multiple sources that vary in sucrose concentration (Tamm and Gass 1986, González-Gómez and Vásquez 2006). Moreover, they are able to match their foraging visits with nectar-renewal schedules (Gill 1988, Garrison and Gass 1999, Henderson et al. 2006). In this context, the aim of our study was to evaluate individual flexibility of feeding intervals in hummingbirds and to assess the relationship between foraging interval and nectar-renewal rates and its effect on individual energy intake. Henderson et al. (2006) studied foraging timing in free-living Rufous Hummingbirds (*Selasphorus rufus*) by assessing their ability to recall two nectar-renewal rates in the field. We did a similar field experiment with the Green-backed Firecrown (*Sephanoides sephaniodes*; hereafter "firecrown"), a migratory hummingbird that winters in central Chile and experiences field temperatures from 30°C (March) down to –5°C (August) (di Castri and Hajek 1976). At –5°C, thermoregulatory cost for these birds is about 5.2× above basal costs (López-Calleja and Bozinovic 1995). In a second experiment, we assessed the ability of firecrowns to remember nectar-renewal rates of visually identical artificial flowers with high and low nectar concentrations; these concentrations were chosen to reflect the fourfold variation in sugar concentration previously recorded at the study site (Smith-Ramirez 1993). If firecrowns can match their foraging intervals to nectar-replenishment schedules, we expected that the time between visits to artificial flowers with short nectar-replenishment intervals would be significantly shorter than the interval between visits to flowers with long nectar-replenishment schedules. Furthermore, if firecrowns can integrate information on nectar-renewal rates and nectar quality, we expected that they would match their foraging intervals to variation in nectar concentration and renewal rates and, thus, maximize energy intake.

Methods

Species and study site.—The study was conducted during June and July 2007 and 2008 at a site in the Andean foothills within the Estación de Investigaciones Ecológicas Mediterráneas of the Pontificia Universidad Católica de Chile, San Carlos de Apoquindo, central Chile (33°23′S, 70°31′W; 1,100 m a.s.l.), ~20 km east of Santiago. The vegetation at the study site is primarily sclerophyllous evergreen scrub known as "matorral." Between March and August, temperatures can fluctuate from >30°C to –5°C. The climate and habitat of the study site are described in detail online (see Acknowledgments).

Experiment 1: One Nectar Quality, Two Nectar-renewal Rates, Free-living Territorial Males

We studied 6 free-living territorial male firecrowns to assess their ability to match foraging visits to different nectar-renewal rates. Individuals were identified on the basis of feather pattern and conspicuous territorial behavior. Subjects included in the analysis were visible to a single observer at all times during the trials (González-Gómez and Vásquez 2006). Because individuals of this species defend territories aggressively, and because territories are small (~200 m²), we could record an individual's behavior continuously over the course of a half day (0730–1200 hours). On any given day, we selected individuals with territories ≥40 m apart to avoid interactions between focal individuals. We ended the trial and did not include data in the analysis if we lost track of a subject during the trial. Observations were made from hidden spots behind vegetation that were ≥10 m from the feeder.

Initial training.—The experiments included a training period during which the subjects became accustomed to the feeders and defended them actively as part of their territories. We placed training feeders that contained 100 mL of 20% (weight/weight) sucrose in six trees (*Quillaja saponaria*, *Litraea caustica*, and *Eucalyptus globulus*) that were 5–15 m tall. Feeders were placed 1.5 m above the ground in locations where we had previously observed territorial firecrowns. Each feeder was filled twice a day to prevent resource depletion that could lead to cessation of territorial defense (González-Gómez and Vásquez 2006), and each male defended one feeder actively as part of his territory within 2 days of deploying the feeders. We observed only one dominant male per feeder. An artificial feeder consisted of a commercial glass water dispenser (for squirrels) enveloped with red paper.

Experimental protocol.—To present firecrowns with nectar-renewal schedules, we replaced the training feeder with two groups of 10 artificial flowers each ($n = 20$). All the flowers contained the same sucrose concentration (22.5% w/w). An artificial flower was designed from an orange syringe tip on which red paper petals were mounted horizontally in an empty training feeder (Fig. 1). Each flower contained 10 μL of the sucrose solution. Within a group, flowers were spaced 10 cm apart. Both groups of flowers were located in a 50×50 cm vertical grid (Fig. 1). The grid was hung 1.5 m from the ground from a branch within the focal territory. We randomly selected one group of flowers to be refilled every 10 min after the flowers were drained (hereafter "short-interval flowers") in every territory. The other group was refilled every 20 min (hereafter "long-interval flowers"). The artificial flowers were filled manually. To prevent firecrowns from using the filling bouts as a visual cue of nectar-renewal rate, we randomly performed five sham fillings per trial. The observer went through the motions of refilling the flowers without actually doing so during sham fillings at time intervals inconsistent with the assigned
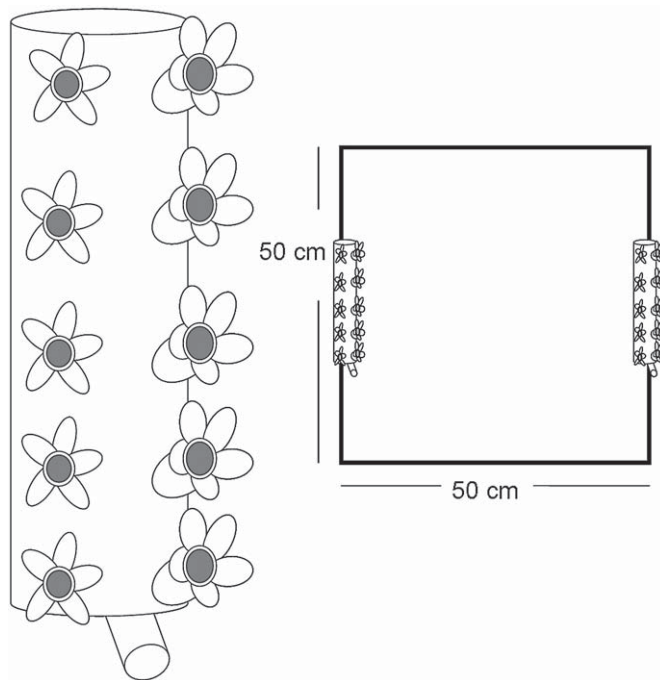
Fig. 1. Diagram of the experimental setup used in the first experiment. Two experimental groups of flowers (short and long intervals) were located in the experimental vertical grid used in the first experiment (right). On the left is an enlarged view of one group of flowers.

nectar-replenishment schedule. A visit was defined as a focal individual inserting its bill into the feeder. In general, all flowers in a group were visited and emptied during each visit. We recorded a focal individual's foraging intervals from 0830 to 1130 hours. However, we considered the first hour to be a training period and included only the last 2 h of data in our experimental analysis.

Experiment 2: Two Nectar Qualities, Two Nectar-renewal Rates, Aviary-housed Males

We conducted an experiment on 6 firecrowns (mean body mass ± SE = 6.0 ± 0.89 g) held in a 6.0 × 6.0 × 5.0 m aviary that was exposed to field temperatures in order to perform a more controlled assessment of the ability of firecrowns to remember nectar qualities associated with nectar-renewal rates. Air temperatures during the trials (5.6 ± 0.60°C, $n = 3$ per trial) were recorded using three data loggers. Temperatures were similar to field temperatures (5.1 ± 0.58°C, $t = 0.10$, df = 18, $P = 0.91$) and did not differ significantly among experimental days (repeated-measures analysis of variance [ANOVA], $F = 2.37$, df = 5 and 12, $P = 0.08$). We caught and tested the individual birds one at a time. Every subject experienced a 12-h training period during which it acclimated to the artificial feeders and aviary. During the training period, we dispensed nectar ad libitum in training feeders described above (see Experiment 1).

To test the ability of firecrowns to match their foraging intervals to variation in nectar qualities and renewal rates, we offered two patches of identical artificial flowers, with four flowers in each.

The flowers of one patch were refilled every 3 min with low-quality nectar (15% w/w sucrose), whereas the flowers in the other patch were refilled every 6 min with high-quality nectar (30% w/w sucrose). Separate nectar-dispensation systems were used to fill flowers in each of the two treatment groups. Each dispenser was composed of a reservoir of nectar (500 mL) connected to a solenoid valve connected to a computer that automatically dispensed a 60 ± 0.01 μL portion[-1] of nectar to each flower in a patch at the appropriate time interval. The 60-μL volume was small enough to be consumed in one visit. Nectar feeders consisted of a glass medicine dropper (5 cm long and 3 mm diameter at the tip) enveloped in red paper to simulate artificial flowers. Because the solenoid valve produced a low intensity but audible noise, we isolated the valve in a polystyrene box so that the sound was not audible to the human ear. We further masked any remaining sound with white noise using an air pump during the experiments.

To avoid nectar accumulation in unvisited feeders, we inserted a second hose into each feeder that expelled air and caused the nectar in the droppers to fall out if not consumed within 60 s of being dispensed. All feeders of one quality ($n = 4$) were located 10 cm apart on a 150 × 100 cm plastic grid that was placed vertically in the aviary 2 m above the ground. Each feeder was located at a 45° angle with respect to the grid. The other group of feeders ($n = 4$) was located in another identical grid contiguous with the first one. A feeder visit was defined as a subject inserting its bill into the feeder. We recorded the rate of return to feeders over a 4-h period (0730–1130 hours); the first 3 hours were treated as a training period and only data from the last hour were used for analysis.

Statistical Analysis

In the first experiment, we assessed the effect of nectar-renewal rates on the foraging intervals of firecrowns and differences between individuals using nested ANOVA (Zar 1999). Assumptions of normally distributed data and homoscedastic variances were met, and temporal autocorrelation analysis was not significant (Spearman correlation, $P > 0.05$ for all individuals). Individual differences in the ratio of visits to low- and high-nectar-concentration flowers were tested against $H_0 = 1$ and $H_0 = 2$ with a binomial test (Zar 1999).

In the second experiment, we tested for individual differences in the number of visits to both grids using repeated-measures ANOVA (Sokal and Rohlf 1995); the data met normality and homoscedasticity assumptions. We assessed differences between individuals in the number of feeders visited in every grid using repeated-measures ANOVA followed by a Tukey's multiple-comparison test (Zar 1999). We used the Wilcoxon matched-pairs test (Zar 1999) to assess differences in the number of feeders that each individual visited in the high- and low-quality grids because the data were not normally distributed. For each subject, we tested the difference between the mean number of foraging intervals and nectar availability (3 min for low-quality and 6 min for high-quality) using a t-test for a single mean (Zar 1999). We tested for an association between nectar preference (number of feeders visited per foraging bout) and foraging intervals using a one-sample Hotelling's T-square, which tested the performance of each bird against a theoretical expected vector of values (Zar 1999). We tested for differences in mean energy intake among individuals
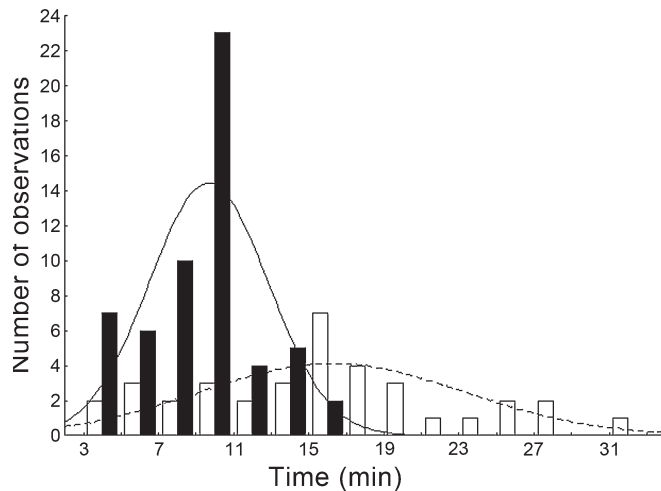
FIG. 2. Frequency distribution of visits to long-interval (i.e., 20 min; white bars and dashed line) and short-interval (i.e., 10 min; black bars and solid line) nectar feeders by Green-backed Firecrowns. Lines represent normal distribution adjustment. The frequency of visits did not differ significantly from a normal distribution (Kolmogorov-Smirnov goodness-of-fit test: long intervals, $d = 0.10$, $P = 0.2$; short intervals, $d = 0.14$, $P = 0.2$).

per trial using repeated-measures ANOVA and Tukey's HSD test as post hoc tests for unequal sample sizes. We performed all statistical analyses using STATISTICA, version 6.0 (StatSoft, Tulsa, Oklahoma). Results are presented as means ± SE.

RESULTS

Experiment 1.—The interval between foraging visits did not differ significantly among free-living firecrowns (nested ANOVA, $F = 0.67$, df = 1 and 5, $P = 0.74$), and therefore we combined data from all subjects for further analysis. Individuals visited short-interval feeders at significantly shorter intervals (9.2 ± 0.45 min) than long interval feeders (16.2 ± 1.18 min; nested ANOVA, $F = 41.02$, df = 1 and 5, $P < 0.01$; Fig. 2). However, the 10-min feeders were not visited twice as often as the 20-min feeders (ratio of visits to 10:20 min feeders: 1.76, tested against $H_0 = 1$, $P < 0.001$; tested against $H_0 = 2$, $P < 0.05$).

Experiment 2.—The number of visits to the grid containing high-quality nectar feeders (7.5 ± 0.88) did not differ significantly from the number of visits to the low-quality grid (3.7 ± 2.17; repeated-measures ANOVA, $F = 2.17$, df = 1 and 5, $P = 0.2$). The number of feeders visited per grid was significantly higher on the high-quality grid (2.4 ± 0.16) than on the low-quality grid (0.4 ± 0.22; repeated-measures ANOVA, $F = 7.4$, df = 1 and 5, $P = 0.04$). Individually, 4 birds fed from more feeders per visit to the high-quality grid than to the low-quality grid (Wilcoxon matched-pairs test, $P < 0.05$ for birds 3, 4, 5, and 6; Fig. 3). By contrast, individuals 1 and 2 visited similar numbers of feeders in each grid, irrespective of nectar quality (Wilcoxon matched-pairs test, $P = 0.67$ and $P = 0.37$, respectively; Fig. 3).

Individuals 1 and 2 visited the low-quality grid at intervals very close to what would be expected for maximization of energy
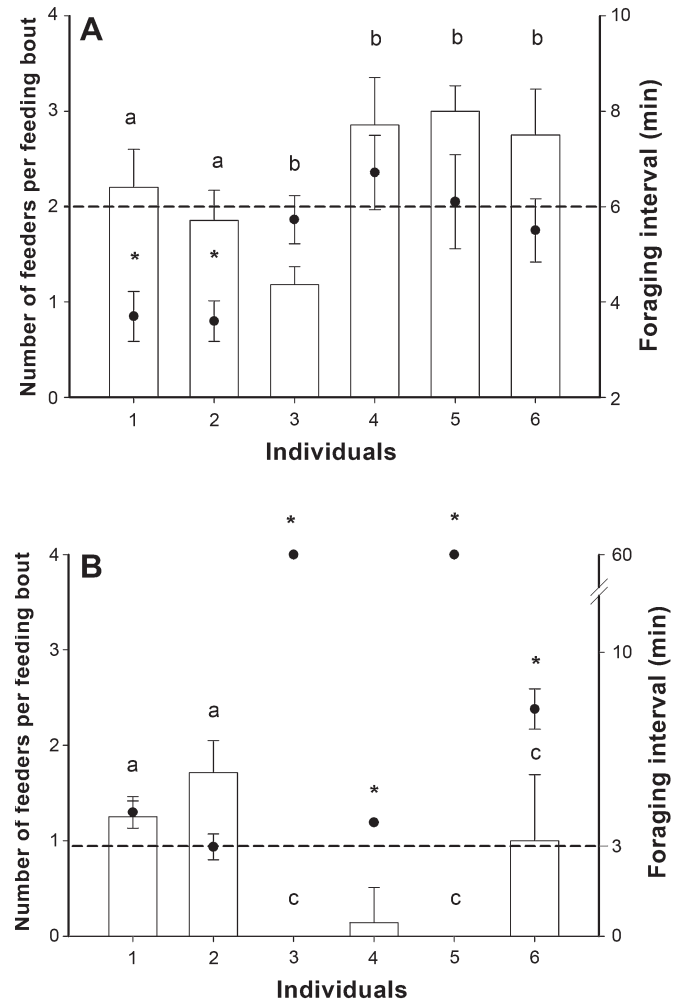

FIG. 3. (A) Number of feeders visited (bars, mean ± SE) and foraging intervals (points, mean ± SE) performed in the visits to the high-quality grid. Dashed line represents the high-quality nectar-renewal rate of 6 min. (B) Number of feeders visited (bars, mean ± SE) and foraging intervals (points, mean ± SE) performed in the visits to the low-quality grid are shown. Dashed line represents the low-quality nectar-renewal rate of 3 min. The discontinuous *y*-axis at the right of panel B represents two individuals that never visited the low-quality feeders. Asterisks indicate significant differences ($P < 0.05$) between nectar availability (i.e., 6 min or 3 min) and individual foraging intervals (*t*-test for a single mean). Letters show significant differences ($P < 0.05$) in the number of feeders visited per grid among individuals (Tukey's HSD test, multiple comparisons).

harvest on the low-quality nectar ($T^2 = 2.490$, $F = 2.490$, df = 1 and 2, $P = 0.5$; Fig. 3). These same individuals failed to match their visitation rate on the high-quality grid to what would be expected for maximization of energy harvest on the high-quality nectar ($T^2 = 174.96$, $F = 174.96$, df = 1 and 3, $P < 0.01$).

The grid-visitation intervals of individuals 3, 4, 5, and 6 did not differ significantly from expected values for maximization of energy harvest from high-quality nectar feeders ($T^2 = 0.417$, $F = 0.417$, df = 1 and 6, $P = 0.5$; Fig. 3) but differed significantly from
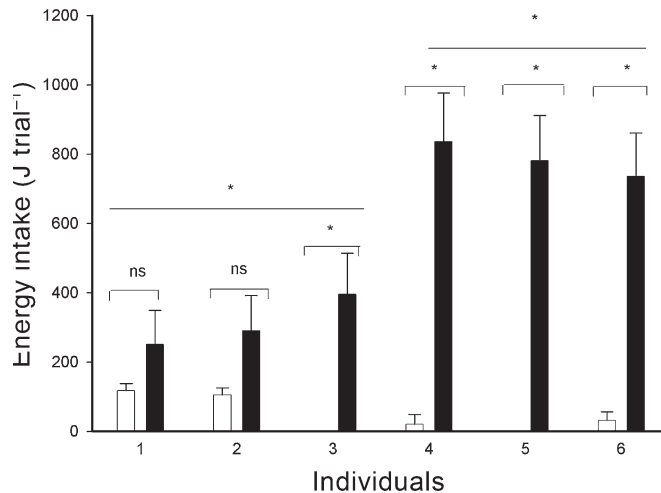
Fig. 4. Energy intake per individual per visit (mean ± SE). White bars show energy obtained from consumption of low-quality nectar (15% w/w sucrose). Black bars show energy obtained from consumption of high-quality nectar (30% w/w sucrose). Asterisks indicate significant differences ($P < 0.05$), and ns = nonsignificant ($P > 0.05$) (Tukey's HSD test, multiple comparisons for unequal sample sizes).

expected values for maximization of energy harvest from low-quality nectar feeders ($T^2 = 219.39$, $F = 219.39$, df = 1 and 6, $P < 0.05$).

The individuals that both matched their visitation intervals to the renewal interval of the high-quality grid and then visited the most feeders per grid visit (i.e., individuals 4, 5, and 6) achieved the highest energy gain per trial (repeated-measures ANOVA, $F = 3.42$, df = 5 and 63, $P < 0.01$; Fig. 4).

Discussion

The ability to determine temporal associations to maximize energy intake rates is a central trait in the foraging ecology of nectarivorous animals (Healy and Hurly 2004). Our results strongly suggest that free-living firecrowns are able to recall different nectar-renewal rates and match their foraging intervals to nectar availability in the absence of visual cues. These results are consistent with previous studies of traplining Hermit Hummingbirds (*Phaethornis* spp.) that showed their ability to match their foraging visits to one fixed-interval schedule of food presentation (Gill 1988, Garrison and Gass 1999). Additionally, the subjects in our study performed better when they recalled shorter intervals, which is consistent with a similar study in territorial Rufous Hummingbirds (Henderson et al. 2006). High variance in the ability to remember distributions of longer intervals agree with scalar expectancy theory (Gibbon et al. 1977), which shows that the variance of remembered distributions increases with the magnitude of intervals between rewards.

Because hummingbird foraging ecology is closely linked to floral nectar dynamics, cognitive abilities (e.g., timing) are expected to have evolved to facilitate efficient nectar exploitation (Cole et al. 1982, Wolf and Hainsworth 1990). However, an animal that uses flowers as a food resource needs to be able to remember additional elements (i.e., quality and location) and to combine these elements in order to efficiently harvest nectar (Henderson et al. 2006). When the subjects in our study were confronted with different nectar qualities and renewal rates, some individuals matched their foraging intervals with this nectar availability. Contrary to our expectations, other individuals matched their foraging visits to availability of low-quality nectar. One possible explanation is the existence of different strategies in the population owing to risk aversion or territory-defense costs. Although this experiment did not incorporate nectar variance, some subjects take more time to acquire information about the environment (Groothuis and Carere 2005, Elmore et al. 2009, Minderman et al. 2009) and shorter-interval flowers may be assessed by these subjects as a lower-risk food source than richer flowers that are available at longer time intervals. Experiments performed with pigeons and primates show that the length of delay to access to food has an important influence on their choices; animals subjectively devalue rewards as the delay increases (Ainslie 1974, Rosati et al. 2006). Additionally, previous studies have reported that hummingbirds show conventional risk-averse behavior and select the constant reward over the low- or high-variance rewards (Hurly and Oseen 1999; but see Bateson 2002).

On the other hand, the cost of territoriality could determine the strategy used by an individual. Following the cost–benefit approach, the energy derived from the exclusive access to the resources in a territory should be greater than the cost of the defense (Brown 1964). In the field, territorial hummingbirds maintain their feeding territories free of intruders by performing chases and vocalizations, both of which are energetically expensive behaviors (Powers and Conley 1994). Camfield (2006) found that hummingbirds engaged in more energetically expensive behaviors when they defended high-quality sites. Additionally, a higher level of territorial display increased intruder pressure and competition for a food source (Powers 1987, Marchesseault and Ewald 1991). Therefore, some subjects could reduce competition, and avoid its cost, by choosing lower-quality territories. Although this experiment was carried out in the absence of competition, it is possible that both observed behaviors (i.e., matching with low or high nectar quality) could be present in the population.

Differences in individual performance translated into differences in total energy obtained. This suggests differences in information use, perhaps tied to individual cognitive abilities. Those differences could produce fitness variability in an energetically demanding context. Hummingbird species that inhabit temperate zones, such as *S. sephaniodes* in central and southern Chile, experience a wide range of temperatures and, consequently, their thermoregulatory costs and foraging demands vary greatly (López-Calleja and Bozinovic 1995, Fernández et al. 2002). In this context, the rate of net energy gain is important because high metabolic rates make energy storage more difficult for hummingbirds (Hainsworth 1978). Territorial males may increase their foraging opportunities and, therefore, their chances of surviving a hard winter if they have the capacity to recall the sugar content and location of a flower and to predict the time when the flower will have the maximum quantity of nectar. Our results strongly suggest that individual foraging strategies may play a central role in determining individual net energy gain and, by extension, fitness.

Nevertheless, conclusions about the success of different individual foraging choices (i.e., low-quality short intervals or high-quality long intervals) must be tested in the field so that the rate of energy gain can be compared with the costs associated with territorial defense, competition, and travel time among patches. These different strategies may all have similar performance under the more complex circumstances experienced by free-living birds, even though they appear to differ rather dramatically in the simplified captive environment. The evaluation of these different possible explanations for the variation observed in our study would require further field studies to determine whether multiple distinct strategies indeed exist in the population, and their degree of individual plasticity.

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